

# The Middle Triassic Megafossil Flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 4. Umkomasiaceae. *Dicroidium* and Affiliated Fructifications

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Holmes, W.B.K. and Anderson, H.M. (2005). The Middle Triassic megafossil flora of the Basin Creek Formation, Nymboida Coal Measures, New South Wales, Australia. Part 4. Umkomasiaceae. *Dicroidium* and affiliated fructifications. *Proceedings of the Linnean Society of New South Wales* **126**, 1-37.

The forked leaves of the morpho-genus *Dicroidium* are the most commonly occurring foliage in the collections from two quarries in the Middle Triassic Basin Creek Formation at Nymboida, N.S.W. The extensive Nymboida collections include leaves which, in gross morphology, range from simple with entire margins to pinnatifid, pinnate, bipinnatifid and bipinnate forms. The wide range of variation, which includes intergrading forms, creates problems in establishing species boundaries. For comparison with other Gondwanan material, the Nymboida leaves have been placed in five 'species complexes' distinguished as '*Dicroidium coriaceum*', '*D. odontopteroides*', '*D. lineatum*', '*D. dubium*' and '*D. zuberi*'. In each complex there is a continuum of variation of form and there are intergrading forms that link each complex. Illustrations of over eighty leaves demonstrate the range of variation present. A single leaf only of *D. elongatum* has been collected. An unusual leaf is described as ?*D. nymboidense* sp. nov. Fertile material affiliated with *Dicroidium* includes three species of female strobilus, *Umkomasia distans*, *U. sessilis* and *U. sp. A.* together with dispersed cupules and ovules. Microsporophylls are placed in *Pteruchus* sp. cf. *P. matatamajor* and a single specimen in *P. sp. A.*

Manuscript received 17 February 2004, accepted for publication 18 August 2004.

Keywords: *Dicroidium*, Middle Triassic flora, Nymboida Coal Measures, *Pteruchus*, *Umkomasia*.

## INTRODUCTION

This is the fourth in a series of papers describing the rich and diverse Middle Triassic megafossil floras from two quarries located near the village of Nymboida in north-eastern New South Wales. A locality map showing the Coal Mine and Reserve Quarries and a summary of the geology of the Nymboida Sub-basin was included in Part 1 (Holmes 2000), which also dealt with the Thallophyta and Sphenophyta. Part 2 (Holmes 2001) included descriptions of 14 taxa of the Filicophyta known from material preserved in a fertile state or remains of sterile material with known fern relationships. Twenty four morpho-taxa of fern-like leaves of unknown relationships were described in Part 3 (Holmes 2003).

In this paper abundant material of the leaf

morpho-genus *Dicroidium* and its affiliated male and female fructifications, *Pteruchus* and *Umkomasia* respectively, from the two Nymboida localities is described and illustrated.

## A history of *Dicroidium*

*Dicroidium* appeared first in the Middle Early Triassic (Smithian), becoming more numerous and diverse in the Middle and Late Triassic (Ladinian to Carnian) of the Gondwana super-continent (Retallack 1977, Anderson and Anderson 1983). There are no reliable Jurassic records (Anderson and Anderson 2003, p.243) and the genus is presumed to have become extinct at the Triassic-Jurassic boundary. The success and diversification of the genus is recorded in numerous publications since the first description and illustration of three leaf fragments from Tasmania

by Morris (1845, as *Pecopteris odontopteroides*). The genus *Dicroidium* was erected by Gothan (1912), who recognised that the forked Gondwanan leaves, usually referred to *Thinnfeldia*, were distinct from the unforked leaves of the Northern Hemisphere. Walkom (1917) retained the name *Thinnfeldia* and later erected the genus *Johnstonia* (Walkom 1925b) for simple forked fronds from Tasmania.

In an overview of genera attributed to the 'Thinnfeldia' series, in which he accepted *Dicroidium*, Frenguelli (1943) also erected the new genera *Dicroidiopsis*, *Diplasiophyllum*, *Xylopteris* and *Zuberia* for Gondwana forked leaves. Townrow (1957) and Archangelsky (1968) synonymised Frenguelli's new genera with *Dicroidium*. Retallack (1977), in a biostratigraphical review of *Dicroidium* and allied genera, retained *Johnstonia* and *Xylopteris*. Anderson and Anderson (1983), in their extensive study of *Dicroidium* in the Molteno Flora (South Africa), provided a detailed historical review, references and comprehensive lists to 1982 of all the illustrated material from Gondwana that they considered to fall within the genus. They also discussed synonyms and forking fronds distinct from *Dicroidium*.

Gothan (1912) studied the cuticle of *Dicroidium* and showed that it was distinct from *Thinnfeldia*. Jacob and Jacob (1950) and Townrow (1957) added further evidence for the separation. Anderson and Anderson (1983) carried out a comprehensive cuticular study (light and scanning electron microscopy) on *Dicroidium* in the Molteno Formation. Based on permineralised material from Antarctica, Pigg (1990) and Boucher et al. (1993) have described the anatomy of *Dicroidium* leaves. The permineralised fructifications, *Pteruchus* and *Umkomasia*, have been described by Yao et al. (1995) and Slavins et al. (2002) respectively.

While the forked leaves of *Dicroidium* are ubiquitous in Gondwana Triassic floras (Retallack 1977; Anderson and Anderson 1983) their origin is unresolved (Boucher et al. 1993; Axsmith et al. 2000). Archangelsky (1996) suggested that the Carboniferous pteridosperm *Botrychiopsis* may provide a plausible ancestral morphology for the Umkomasiaceae. Retallack (1980) noted that the multi-forked *Lepidopteris callipteroides*, which occurs immediately above the Late Permian coal seams in the Sydney Basin, probably belonged to the pteridosperm stock that gave rise to *Dicroidium*, most likely through intermediate forms similar to '*Dicroidium*' *gopadense* from Nidpur in India (Bose and Srivastava 1971). Palaeozoic pteridosperms from Siberian and Cathaysian sources that survived the end-Permian extinction in refugia as yet unidentified

should also be considered. Since Thomas (1933) first suggested *Umkomasia* as a possible early angiosperm this has been much debated and remains unresolved (see Slavins et al. 2002 for a recent discussion).

Thomas (1933) placed *Dicroidium* and its affiliated fertile organs in the Family Corystospermaceae. This family name has been widely used but according to ICBN rules a family must be based on the ovulate genus, in this case *Umkomasia* and therefore Umkomasiaceae. Meyen (1987) placed the Family Umkomasiaceae and the Class Umkomasiales in the gymnosperm Order Ginkgoopsida. Anderson and Anderson (2003), in their recent review of *Umkomasia* and *Pteruchus* from the Molteno Flora, followed this classification.

### The question of *Dicroidium* attachment

While the leaves of *Dicroidium* are abundant and widespread throughout Triassic Gondwana, the form of a whole plant is still debated. Various authors have suggested that *Dicroidium* ranged from shrubs to tall trees (Retallack 1980; Anderson et al. 1998; Anderson and Anderson 2003) or was a large tree (Taylor 1996). Petriella (1978) reconstructed *Dicroidium* as a palmiform tree to 10m high. The reconstruction by Retallack and Dilcher (1988, fig. 10) showed a tall deciduous forest tree in a seasonally wet lowland.

Despite the large numbers of *Dicroidium* leaves preserved in the Nymboida sediments, no leaves have as yet been found attached to a stem. The only convincing specimen elsewhere of leaves attached to a stem was illustrated by Anderson and Anderson (1983, Pl. 88, fig. 1). Another incomplete specimen (Anderson and Anderson 1983, Pl. 88, fig. 2) suggested that the leaves were attached in a fascicled manner to a stem. Anderson and Anderson (2003 p. 257, text fig. 5) base their reconstruction on these specimens.

In a paper describing *Umkomasia uniramia*, Axsmith et al. (2000, figs 6 and 8) illustrated a *Dicroidium odontopteroides* leaf apparently contiguous with, or overlain by, a stem of a plant with long and short shoot morphology. By analogy with extant plants bearing long and short shoot morphology (e.g. *Ginkgo biloba*) it would be unlikely in the extreme for a plant with this growth morphology to bear a leaf on the long shoot section of a stem subsequent to the formation of well-developed short shoots. On the illustrated Antarctic specimen even the short shoots are in a leafless state. The close association of the *Dicroidium* leaf and stems bearing short shoots suggests an affiliation but this is not exclusive as other leaves (e.g. *Heidiphyllum*, *Taeniopteris*) are present in the same deposit. We do



not accept the claim of Axsmith et al. (2000) that their specimen “demonstrates unequivocal evidence” of *Dicroidium* attachment.

Archangelsky (1968) argued a case for the affiliation of silicified logs of *Rhexoxylon* and *Dicroidium* leaves. Meyer-Berthaud et al. (1993) described permineralised twigs from Antarctica as *Kykloxylon* and suggested that the stems bore *Dicroidium fremouwensis* Pigg (1990) leaves, but in neither of these cases have the leaves been found in organic connection.

### ***Dicroidium* and its fertile organs**

Thomas (1933) described the female organ *Unkomasia* and the male *Pteruchus*. Based on close association and similarity of cuticles he regarded them as the fructifications of *Dicroidium*. This affiliation is now generally accepted (Townrow 1962; Holmes 1982; Anderson and Anderson 1983, 2003; Crane 1985; Retallack and Dilcher 1988; Yao et al. 1995 and Slavins et al. 2002).

The fertile genera *Karibacarbon* (Lacey 1976, Holmes and Ash 1979) and *Fanerotheca* (Anderson and Anderson 2003) have also been linked to *Dicroidium*. The species described by Axsmith et al. (2000) as *Unkomasia uniramia* from Antarctica is an ovulate organ with single pedicillate cupules arranged in a terminal radial whorl on a peduncle attached to a leafless short shoot on a mature stem bearing further leafless short shoots. From the significant differences in the architectural arrangement of this fructification we believe it should be placed in a morpho-genus separate from *Unkomasia*.

### **Problems with *Dicroidium* taxonomy**

In many early records (Walkom 1917, Frenguelli 1943) the forked leaves now known as *Dicroidium* (Gothan 1912) were placed in several genera and particularly in *Thinnfeldia*. Walkom (1917) considered his “*Thinnfeldia*” leaves to be ferns as they were closely associated with frond fragments bearing sori. Townrow (1957) separated these fertile fragments from *Dicroidium* as they were indeed ferns which Holmes (2001) has placed in the new genus *Herbstopteris*. Several genera of forked fronds have been described as separate from *Dicroidium* based mainly on morphological differences of pinna or pinnule shape (eg *Johnstonia*, *Xylopteris*, *Zuberia* and others). Townrow (1957), Archangelsky (1968), Holmes (1982) and Anderson and Anderson (1983, 2003) have regarded most of these additional genera as synonyms of *Dicroidium*. Leaves illustrated by Anderson and Anderson (1983, Pl. 74, figs 1-9) which showed typical *D. elongatum* (= *Xylopteris elongata*)

pinnae and typical *D. odontopteroides* pinnae on the same leaf indicate how closely related these ‘genera’ are. It is far more likely that those leaves are interspecific rather than intergeneric ‘hybrids’ or even one polymorphic species. Some South American workers continue to use a multiplicity of generic names for *Dicroidium* leaves (Artabe 1990; Artabe et al. 1998; Gnaedinger and Herbst 1998, 2001).

Early authors appear to have worked only on limited museum collections or had very little field experience because they failed to recognise the variability within their ‘species’ and the intergrading forms that may have linked the ‘species’. Holmes (1982) discussed the problems created by the variation and intergrading forms of *Dicroidium* in the Middle Triassic Benolong Flora. He referred to the work of Meyen (1979), who had demonstrated from a large population of Permian pteridosperm leaves previously placed in several genera and many species that they all belonged in the single species *Rhaphidopteris praecursoria*. Rees and Cleal (1993) showed that the leaves of a Jurassic pteridosperm previously placed in six species and four genera all belonged to *Archangelskya furcata*.

The revision by Retallack (1977) of the *Dicroidium* genus (plus *Xylopteris*, *Johnstonia* and *Tetratilon*, which he retained as allied but distinct) was a significant attempt to provide a taxonomic guide to the genus that would mainly be useful for stratigraphic purposes. However, his descriptions and stylised sketches of the taxa he recognised failed to demonstrate the range of variation within a single population of each taxon. The necessity under the IBCN Code (ICBN 2001) for typification has also exacerbated the problem of dealing with variable fossil populations.

The photographic record by Anderson and Anderson (1983) of 1133 individual *Dicroidium* leaves arranged in ‘palaeodemes’ was a notable achievement and clearly demonstrated the diversity within single populations of *Dicroidium* leaves. They were the first to use palaeo-gamma taxonomy for *Dicroidium*, i.e. using the data of comprehensive collections from many localities. They defined a ‘palaeodeme’ as a “collection of specimens representing a single breeding population showing a normal distribution of variation and derived from a single fossil assemblage from a discrete lithological unit”. The same authors did not attempt to define precise boundaries between taxa as they considered “it would be unproductive considering the general morphological fluidity within the genus” and they had “little doubt that *Dicroidium* speciation was anything but simple and came closer to the reticulate speciation model of Sylvester-

Bradley (1977)". Based on the palaeodeme approach, Anderson and Anderson (1983, 1989) listed a total of 32 taxa comprising 10 species, 17 subspecies and 15 formae. In their recent revision (Anderson and Anderson 2003) *Dicroidium* now comprises 21 taxa of specific rank plus 15 formae.

The reasons listed by Boucher et al. (1993) provided a good summary of why *Dicroidium* is not a well-understood genus: there is a large amount of morphological variation; there is inconsistency in naming; variations in cuticular features are not well enough known; complete plants are not known; sample sizes are small especially from remote areas; and often only fragments are preserved.

## MATERIALS

In the Holmes' catalogued collection of over 2600 slabs of Nymboida material, approximately one third of the slabs bear leaves that can be attributed to *Dicroidium*. The female and male fertile organs *Umkomasia* and *Pteruchus* affiliated with *Dicroidium* are rare and have been found at a ratio of one identifiable specimen to c. 70 leaves. This is closely similar to the ratio observed at the Benolong locality (Holmes 1982). In the Molteno assemblages Anderson and Anderson (2003, p. 240, 250) also noted that the fertile organs were rare and gave the return for each locality only in terms of man-hours spent chipping open fossiliferous slabs.

The Nymboida fossil plant material is preserved mostly as carbonaceous compressions, but a tectonic heating event during the Cretaceous (Russell 1994) has destroyed the cuticle of otherwise beautifully-preserved specimens.

In addition to the material held in the Holmes collection we have examined other Nymboida specimens housed in the University of New England Geology Department and the Australian Museum.

## OUR METHOD OF NOMENCLATURE

Earlier attempts to classify Nymboida *Dicroidium* leaves were made from limited and usually fragmentary specimens, i.e. using mainly palaeo-alpha taxonomy (De Jersey 1958, Flint and Gould 1975, Retallack et al. 1977). Retallack (1977 Microfiche Frames G11-G13) listed 12 *Dicroidium* taxa plus one each of *Johnstonia* and *Tetraptilon* (both here included in *Dicroidium*) and two ovulate species from the Coal Mine Quarry.

In this present revision we have used mainly

palaeo-beta taxonomy and based our classification on our comprehensive collection of over 2600 selected and catalogued slabs that have been accumulated during many trips to the Nymboida quarries over a period of almost 40 years. The bulk of the collection was made from fallen blocks that had been blasted or bulldozed from the quarry faces. The exact source of the in situ material is mostly unknown. Except in rare cases such as the slabs containing large numbers of similar leaves (e.g. Figs 2 and 6A), we are unable to identify specific populations or palaeodemes as was achieved by Anderson and Anderson (1983, 1989, 2003). Future work involving in situ collecting from specific assemblages (i.e. from discrete lithological units) would allow palaeo-gamma taxonomy and the material to be documented into palaeodemes.

*Dicroidium* foliage is the most commonly preserved fossil at Nymboida and also in the catalogued collection. The forked leaves occur in a diversity of forms ranging and intergrading from simple leaves with entire margins to pinnate to bipinnate. Faced with this continuum one could place all the leaves in one polymorphic species or, on the other hand, describe numerous species each based on a 'single' type specimen. Due to this range of variation and intergradation we are unable to determine reliable diagnostic features. This makes it difficult to identify the Nymboida *Dicroidium* material to a specific level.

Although the sediments in the Nymboida quarries were deposited over a relatively short period of geological time (Holmes 2000) they do represent many different sedimentary facies, e.g. coal seams, shales, fossil soils, siltstones and sandstones. The enclosed fossils certainly would have been derived from a range of habitats so it is most likely that various species of *Dicroidium* plants had evolved or adapted to occupy particular environmental niches. Only one variable species of *Pteruchus* plus a possible second species are recognised in the Nymboida collections while at least three separate species of the female *Dicroidium* fructification *Umkomasia* are present. It is therefore most likely that several discrete species of plants bearing *Dicroidium* leaves were growing in the region in the Middle Triassic.

For the Nymboida *Dicroidium* leaves to be compared with collections from other geographical and stratigraphical localities we have separated the leaves into informal complexes based on leaf morphology, which range from simple to pinnate, bipinnatifid and bipinnate. Except for the single specimen placed in *D. elongatum* (Figs. 19, 20A) and the few rare and problematic specimens (Figs 20B-E) we have grouped the foliage material into five 'species



complexes' each named for a previously-described species that represents the core of the complex. Specimens in the Selected References lists also have a gross morphology identifiable with the core of the complex. Each complex includes a particular section of the range of diversity of the Nymboidea *Dicroidium* leaf collections and is linked by intergrading forms with adjacent complexes. We illustrate over 80 reasonably well-preserved leaves (Figs 1-18), that demonstrate the variation within each complex and the obvious forms intergrading between successive complexes. While we acknowledge that our form of classification is subjective, it is based on a large and representative collection of reasonably well-preserved material.

Due to constraints imposed by the lack of storage facilities at the Australian Museum only the specimens illustrated in this paper have been allocated AMF numbers. All other specimens remain in the Holmes Collection.

## SYSTEMATIC PALAEOBOTANY

Order	Ginkgoopsida Meyen 1987
Class	Umkomasiales Meyen 1984
Family	Umkomasiaceae Meyen 1984

### Genus *Dicroidium* Gothan 1912

#### Type species

*Dicroidium odontopteroides* (Morris 1845)  
Gothan 1912

#### Synonymy [Synonymised by]:

*Johnstonia* Walkom 1925b [Townrow 1957]  
*Dicroidiopsis* Frenguelli 1943 [Archangelsky 1968]  
*Diplasiophyllum* Frenguelli 1943 [Archangelsky 1968]  
*Zuberia* Frenguelli 1943 [Townrow 1957]  
*Xylopteris* Frenguelli 1943 [Archangelsky 1968]  
*Tetraptilon* Frenguelli 1950 [Anderson and Anderson 1983]  
*Hoegia* Townrow 1957 [Archangelsky 1968]

### '*Dicroidium coriaceum* complex'

Figures 1A-C; 2A-E

#### Selected References

1925b *Johnstonia coriacea*, Walkom, figs 6,7  
1927 *Johnstonia coriacea*, Du Toit, fig. 12D, 13B  
1932 *Johnstonia coriacea*, Du Toit, text fig. 2A  
1967 *Dicroidium coriacium*, Jain and Delevoryas,

Pl. 91, fig. 1

1982 *Dicroidium coriaceum*, Holmes, figs 3C, D

1983 *Dicroidium coriaceum* subsp. *coriaceum*,  
Anderson and Anderson, Pl. 36, figs 3-6; Pl.76,  
figs 1-6

1983 *Dicroidium coriaceum* subsp. *dutoitii*,  
Anderson and Anderson, Pl. 41, figs 1-28; Pl.76,  
figs 12-17

#### Description

Forked leaves of variable length and width, usually entire, sometimes lobed and grading to pinnatifid.

#### Discussion

*D. coriaceum* was first described from Tasmania by Johnston (1887) as *Rhacophyllum coriaceum*. Walkom (1925b) re-examined Johnston's material and transferred it to the new genus *Johnstonia*. He noted that the margins were entire or slightly lobed. Specimens attained a length up to 100 mm above the dichotomy and the breadth of the larger specimens was 10 mm, though in general they were narrower. Antarctic material with leaves having a broad lamina and the fork closer to the apex were described by Townrow (1967) as *D. dutoitii*. He selected as the holotype a leaf illustrated by DuToit (1927, text fig. 12D) from the Molteno Formation of South Africa, which differed quite significantly from the Antarctic specimens. Retallack (1977) placed the Antarctic material in *Johnstonia coriacea* var *obesa* with the South African material retaining the epithet *dutoitii*. Anderson and Anderson (1983) have separated *D. dutoitii* from *D. coriaceum* on palaeodeme evidence at localities in the Molteno Formation although their illustrations show some overlap in leaf dimensions. From South America, Jain and Delevoryas (1967, Pl. 91, fig. 1) illustrated a single slab that encompasses the size range of both above species. Holmes (1982) also noted a wide variation in size range of *D. coriaceum* in the Benolong flora of NSW. The Nymboidea leaves illustrated in Figure 1 are a larger form, ranging from 120-140 mm long and 5-10 mm wide and from entire to lobed, and could be regarded as a form of *D. dutoitii* Townrow (1967). As only three slabs of this larger form are present in the Nymboidea collections and their full range of variation is not known we place them in the *D. coriaceum* complex.

The specimens illustrated in Figures 2A-E and Figure 4C were all collected from a single slab of whitish siltstone. We believe that, with the exception only of the pinnate fragment on the lower left of Fig. 2A, all the other leaves represent a single population. They range in length from c. 40-80 mm long and 3-

7 mm wide. The leaf margins are mostly entire but lobed and pinnatifid forms (Fig. 2E and Fig. 4C) are present. The latter forms intergrade with, and are very close to, the pinnatifid and pinnule coalescing forms of the '*D. odontopteroides* complex'.

**'*Dicroidium odontopteroides* complex'**

Figures 3A-E; 4A-G; 5A-D; 6A; 7A-C; 8A; 9A-C; 10A,D,E

**Selected References**

- 1845 *Pecopteris odontopteroides*, Morris, Pl. 6, fig. 3  
 1890 *Thinnfeldia odontopteroides*, Feismantel, Pl. 26, figs 2, 2a  
 1917 *Thinnfeldia lancifolia*, Walkom, Pl. 7, fig. 2; Pl. 3, fig. 1  
 1975 *Dicroidium odontopteroides*, Flint and Gould, Pl. 3, figs 10, 11  
 1982 *Dicroidium odontopteroides* var. *moltenense*, Holmes, figs 4A, B  
 1983 *Dicroidium odontopteroides* subsp. *orbiculoides*, Umk 111 palaeodeme, Anderson and Anderson, Pl. 42  
 1983 *Dicroidium odontopteroides* forma *odontopteroides*, Umk111 palaeodeme, Anderson and Anderson, Pl. 43  
 1992 *Dicroidium odontopteroides*, Taylor et al., fig. 1  
 2000 *Dicroidium odontopteroides*, Axsmith et al., fig. 3, leaf only  
 2001 *Dicroidium odontopteroides*, Gnaedinger and Herbst, fig. 4E (in gross morphology but with denser venation)

**Description**

Usually once-forked pinnate frond to 160 mm long; pinnae to 40 mm long and 15 mm wide, not basally contracted, ranging from semi-orbicular to broadly triangular, to elongated rectangular or slightly tapering, with rounded or broadly obtuse apex; the longer pinnae with a midrib and alethopteroid venation; shorter rounded pinnae with odontopteroid venation as in Fig. 7C. The specimens illustrated in Figs 7A and B represent the core of this Nymboida complex. The leaf in Fig. 8A is the largest specimen from this complex in the collection.

**Discussion**

Taxonomic confusion has arisen since the original description and illustrations of *Dicroidium odontopteroides* (as *Pecopteris odontopteroides*) by Morris (1845). Only three frond fragments were

illustrated and Morris noted that the specimen (Pl. 6, fig. 4) with more elongate pinnae was probably a variety of the species. When compared with the range of variation encompassed in our *D. odontopteroides* complex, Morris's three specimens show a very limited range of variation as would be expected for this morpho-species. However, due to the lack of understanding of the range of variation that commonly occurs in a single population, leaves similar to Morris's elongated pinna form were raised to specific rank i.e. *Dicroidium lancifolium* (Gothan 1912; Walkom 1917; Frenguelli 1943; and others, see Hypodigm Lists of Anderson and Anderson 1983). The presence of a midrib (alethopteroid venation) in the more elongated pinnae has been regarded by some authors as a specific or varietal diagnostic feature. The form of venation is usually dependent on the length and shape of the pinnae, which varies according to the position on the frond and whether on the inside or outside of the fork. Both odontopteroid and alethopteroid forms of venation may be observed on a single frond. Leaves placed in *D. lancifolium* by several authors are best regarded as long-pinnaed forms of *D. odontopteroides*.

The range of variation of fronds within this Nymboida complex encompasses forms that accord with several published species, subspecies, varieties or forms. On the classification of Retallack (1977, Microfiche Frames I1 to I7) these varieties include *D. odontopteroides* var. *moltenense*, *D. odontopteroides* var. *obtusifolium* and *D. odontopteroides* var. *odontopteroides*.

Specimens with short broad pinnae (Figs 3A-D; 4C, D, G; 7C) agree with leaves from the *D. odontopteroides* subsp. *orbiculoides* palaeodeme of Anderson and Anderson (1983, Pl. 42), which included *D. crassinervis* forma *obtusifolium*, *D. odontopteroides* subsp. *orbiculoides* and *D. crassinervis* forma *crassinervis*. Boucher et al. (1993) separated compression and impression material from Mt Falla in the Beardmore Glacier area of Antarctica into *D. odontopteroides*, *D. lancifolium* and *D. dubium* based on minor morphological and cuticular features, which may have represented a normal range of variation within a single species complex. Frenguelli (1950) erected the genus *Tetraptilon* for *Dicroidium odontopteroides*-like leaves from Argentina in which the frond had a double fork. This feature has been recorded also in *D. odontopteroides* assemblages from Australia (Flint and Gould 1975, Pl. 3, fig. 10; Retallack 1977) and South Africa (Anderson and Anderson 1983, Pl. 87, figs 1,2,4 and 6, Pl. 88, fig. 1). Anderson and Anderson (1983) synonymised the genus *Tetraptilon* with *Dicroidium*. In our collections



these multiple forked fronds comprise c. 1% of the *D. odontopteroides* complex. The forking may result in three, four or five branches, with four branches being the most common (Figs 5A-D and Fig. 6A). On some bedding planes this is the only form of leaf preserved. This suggests that for some trees double-forked leaves were the normal frond and not aberrant as was surmised by Anderson and Anderson (1983, Pls 71, 87) because of their rare occurrence. The slab illustrated in Figure 6A is a good example of the range of variation in a single population of double-forked leaves. A single specimen of a double-forked *D. dubium* (Fig. 6B) has also been collected.

In a recent paper, Gnaedinger and Herbst (2001) recognised the great morphological variability in *Dicroidium* leaves from three Upper Triassic formations in northern Chile. They illustrated a number of examples that indicated an intergrading 'line' from *D. obtusifolium* to *D. odontopteroides* (varieties *moltenense* and *remotum*) to *D. odontopteroides* var. *odontopteroides* to *D. lancifolium* var. *lancifolium*. This range of morphology is here included in our '*D. odontopteroides* complex'.

Leaves illustrated in Figures 9A, B are forms intergrading with extremes from the *D. lineatum* complex.

#### **'*Dicroidium lineatum* complex'**

Figures 10B,C; 11A,B,D; 12A-C

#### **Selected References**

- 1883 *Gleichenia lineata*, Tenison-Woods, Pl. 3, fig. 6; Pl. 8, fig. 2  
 1898 *Thinnfeldia indica* var. *falcata*, Shirley, Pl. 7, fig. 2  
 1917 *Thinnfeldia acuta*, Walkom, Pl. 3, fig. 4  
 1977 *Dicroidium lancifolium* var. *lineatum*, Retallack, Microfiche Frame H17  
 1983 *Dicroidium odontopteroides* subsp. *lineatum*, Anderson and Anderson, Pl. 64, figs 12-29; Pl. 65, figs 1-3; Pl. 79, figs 4, 6  
 1985 *Dicroidium lancifolium* var. *lineatum*, Artabe, Pl. 3, fig. 5  
 1992 *Dicroidium lancifolium*, Taylor et al., fig. 2  
 2001 *Dicroidium lancifolium* var. *lineatum*, Gnaedinger and Herbst, fig. 2, A-E, fig. 3 L

#### **Description**

Forked pinnate leaf to 200 mm long; pinnae elongated-triangular to 35 mm long, tapering to acute apex, broad base, usually decurrent.

#### **Discussion**

This complex is closely allied to the *D. odontopteroides* complex but has been separated on the basis of the decurrent pinnae which taper to an acute apex.

Retallack (1977, Microfiche Frames H17, H18) placed leaves of this complex as a variety of *D. lancifolium*, which we regard as belonging in the '*D. odontopteroides* complex'. Leaves comparable to our '*D. lineatum* complex' were described by Anderson and Anderson (1983) from the Molteno Formation of South Africa as *D. odontopteroides* subsp. *lineatum* but were later raised to specific rank (Anderson and Anderson 2003).

In the Nymboida collection, forms with undulate margins or incipient lobes (Figs 11C; 12A,D) are linking forms with the '*D. dubium* complex' below.

#### **'*Dicroidium dubium* complex'**

Figures 6B; 13A-C; 14A-E; 15A-D; 16A

#### **Selected References**

- 1890 *Gleichenia dubia*, Feistmantel, Pl. 26, fig. 3  
 1908 *Thinnfeldia odontopteroides*, Seward, fig. 4  
 1928 *Thinnfeldia talbragarensis*, Walkom, Pl. 27, fig. 1  
 1947 *Thinnfeldia talbragarensis*, Jones and deJersey, Pl. 1, fig. 5  
 1965 '*Thinnfeldia*' *talbragarensis*, Hill et al., Pl. T4, fig. 6  
 1982 *Dicroidium dubium* var. *dubium*, Holmes, fig. 7D  
 1983 *Dicroidium dubium* subsp. *dubium*, Anderson and Anderson, Pl. 33, figs 21-31  
 1983 *Dicroidium dubium* subsp. *tasmaniense*, Anderson and Anderson, Pl. 44, figs 7-16; Pl. 53, figs 15-20; Pl. 59, figs 1-14; Pl. 60, figs 1-5  
 1983 *Dicroidium dubium* subsp. *switzifolium*, Anderson and Anderson, Pl. 44, figs 17-20

#### **Description**

Forked bipinnatifid leaf; pinnae elongate, tapering to acute apex; margin variously lobed, proximal lobes sometimes separated to the pinna rachis but coalescing distally. Leaves variable in size from 70 - 200 mm long; pinnae in mid-portion of leaf from 15 - 90 mm long, 4 - 15 mm wide.

#### **Discussion**

Fronds of the '*D. dubium* complex' are the most commonly occurring *Dicroidium* fossils at the Nymboida quarries. Leaves that represent the core of this complex (Figs 13C, 14D,E, 15B,C) are bipinnatifid to partially bipinnate and agree well with

the Molteno palaeodemes of *D. dubium* subsp. *dubium* as recognised by Anderson and Anderson (1983, p. 106). Pinnac on the same frond may vary from entire to lobed and pinnate. Specimens with narrower pinnac and undulate margins are intergrading forms with the '*D. lineatum* complex' while the bipinnate forms intergrade with those of the '*D. zuberi* complex' (Fig. 15A). The apical leaf fragment showing large bipinnatifid pinnac (Fig. 16A) may be compared with *D. dubium* var. *australe* (sensu Retallack 1977, Microfiche Frame H8).

### '*Dicroidium zuberi* complex'

Figures 16B,C; 17A-D; 18A

#### Selected References

- 1890 *Thinnfeldia odontopteroides*, Feismantel, Pl. 24, figs 1,2; Pl. 25, figs 1,2  
 1917 *Thinnfeldia feismantelii*, Walkom, Pl. 2, figs 1,2  
 1944 *Zuberia zuberi*, Frenguelli, Pl. 4  
 1975 *Hoegia papillata*, Flint and Gould, Pl. 2, figs 4,5  
 1977 *Dicroidium zuberi*, Retallack et al., Figs A-F  
 1979 *Dicroidium zuberi*, Petriella, Pl. 2, fig. 5  
 1983 *Dicroidium zuberi*, Anderson and Anderson, Pl. 61, figs 1-13; Pl. 62, figs 1-4; Pl. 81, figs 1-5  
 1985 *Dicroidium zuberi* var. *papillatum*, Artabe, Pl. 4, fig. 2

#### Description

Frond bipinnate, small to large, 150 - 600 mm long; pinnules variable in shape, rounded to blunt rhomboid or falcate, inclined towards pinna apex, coalescing distally and apically. Basiscopic pinnules often decurrent on main rachis.

#### Discussion

Leaves of this complex are widespread but not common at the Nymboida localities. Solitary large leaves are sometimes preserved intact in beds of sandstone thus indicating they were tough and resistant to damage during transport. *D. zuberi* is differentiated from *D. dubium* by the presence of pinnules divided to the pinna rachis, but there are numerous intergrading forms with deeply bipinnatifid fronds (Fig. 17A,B).

Retallack (1977, Microfiche Frame G12) listed three varieties of *D. zuberi* from Nymboida based on the pinnule shape of mostly fragmentary material. Our extensive collections clearly demonstrate intergrading forms that link the varieties. Indeed pinnules on the same leaf may include different

varietal types (Figs 16B, 18A). The range of pinnule shapes in the Nymboida '*D. zuberi* complex' supports the decision of Anderson and Anderson (1983) to recognise the previously described *D. zuberi* varieties *feismantelii*, *sahnii*, *barrealensis* and *papillatum* as normal variations within a single species.

We agree with Archangelsky (1968), Retallack (1977) and Anderson and Anderson (1983, 2003) that the continued placement of these leaves into the separate genus *Zuberia* (Artabe 1990; Gnaedinger and Herbst 2001) is not warranted.

### *Dicroidium elongatum* (Carruthers) Archangelsky

1968

Figures 19, 20A

#### Holotype

Designated by Retallack (1977) *Sphenopteris elongata* Carruthers 1872, Pl. 27, fig. 1

#### Selected References

- 1883 *Trichomanides spinifolium*, Tenison-Woods, Pl. 3, fig. 7  
 1898 *Trichomanides elongata* var. *spinifolia*, Shirley, Pl. 5, fig. 2  
 1917 *Stenopteris elongata*, Walkom, Pl. 6, figs 1, 3  
 1965 *Xylopteris spinifolia*, Hill et al., Pl. T5, fig. 7  
 1977 *Xylopteris spinifolia*, Retallack, Microfiche Frames J13, 14  
 1982 *Dicroidium spinifolium*, Holmes, Fig. 5B,C  
 1983 *Dicroidium elongatum* forma *remotifolium*, Anderson and Anderson, p. 115, Pl. 48, figs 24-32

#### Description

Known only from a single incomplete specimen from the Coal Mine Quarry (AMF125082). Frond bipinnate, c. 120 mm long; pinnac linear at c. 45° to main rachis; pinnules well-spaced, elongated triangular to linear.

#### Discussion

This solitary specimen is preserved in siltstone together with other fragments that appear to have been subjected to long distance transport before burial. In the probable contemporary Benolong Flora (Holmes 1982) leaves of a '*Dicroidium elongatum* complex' comprised 20% of the preserved plant remains. Holmes reconstructed the Benolong environment as a dry sclerophyll woodland on low fertility sandy soils. The presence of a rich fern and fern-like leaf flora at Nymboida (Holmes 2001, 2003) suggests a vegetation growing in a moist environment with rich soils. This solitary specimen of *D. elongatum*



together with associated plant fragments was most likely transported from a drier less fertile upstream source.

*D. elongatum* is a species complex of pinnate to tripinnate intergrading forms. In the past the various forms have been separated into species, subspecies and formae. Jones and de Jersey (1947) considered the pinnate to tripinnate forms to represent an evolutionary series but all forms are now known to occur together. Holmes (1982) noted that leaves with intergrading characters of most forms were present in the Benolong Flora.

**? *Dicroidium nymboidense* Holmes sp. nov.**

Figure 20B

**Diagnosis**

A small pinnate frond; pinnae few, large elongate-ovate, rounded, irregularly lobed; venation odontopteroid, two decurrent veins entering each pinna then dividing acutely up to five times to form parallel venation to the pinna apices.

**Description**

This new morpho-taxon is based on a single frond impression and counterpart. Frond pinnate, 115 mm long with base missing; curving rachis with five opposite pairs of pinna and a terminal pinna, increasing in size apically; fifth pair of pinnae to 55 mm long, 25 mm wide, elongate-ovate with two or three broad irregular obtuse lobes; texture of pinnae thin, venation conspicuous; two veins enter each decurrent pinna at c. 30°, arch and divide from three to five times then run parallel to each other to pinna apex; the upper of the two primary veins forming a short median vein.

**Holotype**

AMF125083 Australian Museum, Sydney.

**Type Locality**

Coal Mine Quarry, Nymboida. Basin Creek Formation, Nymboida Coal Measures, Middle Triassic.

**Discussion**

This rare and problematical frond is placed with reservations in *Dicroidium*. The rachis curves sideways basally but the leaf base is missing and no fork is preserved. However, on the right margin of the specimen there is a pinnule fragment with venation that divides and runs parallel and is aligned at an angle appropriate for a pinna if it were a portion of a forked *Dicroidium* frond. The venation, while

essentially odontopteroid, is somewhat similar to that in the decurrent, ovate, sometimes lobate pinnules of *Nymboidiantum* spp (Holmes 2003, Figs 17-19). However the size and texture of the pinnae of ?*Dicroidium nymboidense* is unlike that of any *Nymboidiantum* spp. While we are uncertain of its generic placement it is certainly a distinct species and is described and illustrated to draw attention to its presence in the Nymboida Flora.

***Dicroidium* sp. A**

Figures 20C,D

**Description**

Apical portions of two fronds with extremely widely spaced pinnae; Fig. 20C is pinnate, pinnatifid with slightly lobed or entire strongly decurrent pinnae; Fig. 20D is bipinnate with broadly triangular pinnules and basiscopic pinnules decurrent on or attached directly to the main rachis.

**Discussion**

The wide spacing of the pinnae of these incomplete fronds sets them apart from all other more completely preserved fronds. They may possibly represent aberrant forms of *D. dubium* and *D. zuberi* respectively. *D. pinnis-distantibus* (Kurtz) Frenguelli (Retallack 1977, Microfiche Frame M 8) also has very widely spaced pinnae but with entire pinnae margins.

***Dicroidium* sp. B**

Figure 20E

**Description**

The apical portion of a very large bipinnatifid *Dicroidium*-like frond with deeply dentate pinna margins.

**Discussion**

This single portion of an obviously very large frond differs by its size and shape from all other bipinnatifid material from Nymboida. *D. sp. B* differs from the large *D. dubium* var. *australe* (Retallack 1977, Microfiche Frame H8) and *D. dubium* ssp. *helvetifolium* (Anderson and Anderson 1983, p. 105) by the acute triangular pinna lobes. A distal fragment of a somewhat similar-sized but pinnate frond from the Late Triassic Ipswich Basin was attributed by Walkom (1917) to *Danaeopsis hughesi*, now *Dicroidium hughesi* Lele (1962), a species described from India.

Fertile organs associated with *Dicroidium* leaves

Genus *Umkomasia* Thomas 1933

Type species

*Umkomasia macleani* Thomas 1933 p.203, figs 1, 2, 56; Pl. 23, figs 1-4

*Umkomasia distans* Holmes 1987

Figures 21A; 22A

Holotype

AMF 63824, Holmes 1987, fig. 3, fig. 4, A-D

Paratypes

AMF 63825-28

Description

An *Umkomasia* strobilus with widely spaced alternate and spirally arranged branches on an elongate axis; branches with one or two opposite pairs of cupules and a terminal pair or a single cupule; cupules pedicillate, irregularly rounded, 3.5 to 5 mm in diameter.

Discussion

*U. distans* was described and illustrated by Holmes (1987) based on three specimens of reasonably preserved cupule bearing axes from the Coal Mine Quarry, Nymboida. Additional material has been collected (Fig. 21A) but this is fragmentary. For comparisons with other material see Holmes (1987). This species was regarded as distinct from the Molteno species by Anderson and Anderson (2003, Table 51).

*Umkomasia sessilis* Holmes 1987

Figures 21B,C; 22B

Holotype

AMF63829 and counterpart AMF63830, Holmes 1987, fig. 5, fig. 6 A-C

Paratype

AMF63831

Description

An elongate *Umkomasia* strobilus with alternate, spirally arranged branches bearing two pairs of opposite, sessile cupules 4 - 5 mm in diameter.

Discussion

*U. sessilis* differs from *U. distans* by the sessile cupules. *U. decussata* Anderson and Anderson (2003) has sessile cupules but differs by the more numerous pairs of cupules with a decussate arrangement. The partial strobilus located on the lower left hand side of Figure 10A probably belongs here.

*Umkomasia* sp. A

Figure 22C

Description

A portion of a single elongate *Umkomasia* strobilus with well-separated alternate branches, each branch with one or more (?) pairs of cupules borne on long expanding pedicels; cupules strongly decurved, 8-10 mm long.

Discussion

*U. sp. A* differs from *U. distans* and *U. sessilis* by the larger decurved cupules and by the elongated and expanding pedicels. The cupules of *U. gracillaxis* Anderson and Anderson (2003) from the Molteno Formation are decurved and of a size similar to *U. sp. A*. However, their cupules with four lobes each is a feature not preserved on this Nymboida specimen.

Isolated *Umkomasia* cupules

Figures 22D-F

Specimen AMF125092 (Fig. 22D) shows a pair of adjacent and opposite dorsally compressed semicircular cupules each c. 16 mm in diameter, with a 4 mm wide peduncle attached to the proximal margin. These cupules are closely comparable with the cupule shown in a dorsal view of *Karibacarbon* (*Umkomasia*) *feistmantelii* (Holmes and Ash 1979, Fig. 6.2) from the Early Triassic Lorne Basin assemblage and with cupules from the Sydney Basin (Walkom 1925a, Pl. 31, fig. 9; Retallack 1980, fig. 21.9E). No additional specimens have been found at Nymboida to show whether these cupules may have split on dehiscence into several lobes as occurs in *U. feistmantelii* fructifications (Holmes and Ash 1979, fig. 6. 3-5; Walkom 1925a, Pl. 29, fig. 9; 1932, Pl. 5, figs 3-5; Retallack 1980, Fig 21.9F).

Specimen AMF125093 (Fig. 22E) is a thick rounded tapering mass, 15 mm wide, of carbonaceous material attached to a stout peduncle 2 mm wide. On opposite sides of the mass are decurved acute projections. This problematic specimen may represent a pair of large fleshy conjoined cupules, perhaps similar to *Umkomasia* sp. of Retallack (1980, Fig.



21.9E).

Specimen AMF125094 (Fig. 22F) is an isolated dehiscent cupule c. 7 mm wide, split into 24 acute lobes. This cupule was thin textured in contrast to the thick fleshy appearance of the previous specimen. Preservation is too poor to allow for comparisons with known fructifications.

#### Dispersed *Umkomasia* ovules

Figure 21D

Dispersed platyspermic ovules occur frequently on some horizons at both the Coal Mine and Reserve Quarries. The ovules illustrated are c. 5 mm wide and c. 7 mm long, with an acute bifid apex. They are similar in form and shape to the ovules illustrated by Thomas (1933, fig. 33) and Anderson and Anderson (2003, Pl. 82, figs 11-16) and associated with *Dicroidium* leaves at the Umk111 locality of the Molteno Formation. In size they are closest to the ovules associated with *U. quadripartita* from the Mat 111 locality (Anderson and Anderson 2003, Pl. 85, figs 7-10).

#### Genus *Pteruchus* Thomas 1933

##### Type species

*Pteruchus africanus* Thomas 1933, fig. 34, Pl. 24, fig. 71

*Pteruchus* sp. cf *P. matatimajor* Anderson and Anderson 2003

Figures 23A-E

##### Selected references

1947 *Pteruchus* cf *africana*, Jones and de Jersey, text fig. 51

2003 *Pteruchus matatimajor*, Anderson and Anderson, p. 254, Pls 92-94

##### Description

This morpho-taxon is based on the five incomplete strobili illustrated and numerous other detached heads. The main axis is stout, to 2.5 mm wide, length not known; microsporophylls oval to linear-oblong, in pairs on a slender forked peduncle; heads 11-23 mm long, 5-9 mm wide; microsporangia spindle- or cigar-shaped, 2-3 mm long, 0.35-0.5 mm wide, covering whole abaxial surface.

##### Discussion

None of the Nymboida specimens is complete. Figure 23B clearly shows the paired nature of the

microsporophylls. In this feature and size they are closely similar to the *Pteruchus strobilus* illustrated by Jones and de Jersey (1947, text fig. 51) from Ipswich, and also with *P. matatimajor* (Anderson and Anderson 2003) from the Matatiele assemblage in the Molteno Formation. We consider the Nymboida material as close to *P. matatimajor* and quite separate from *P. africanus*, which has smaller unpaired microsporophylls. The identification of *P. dubius* and *P. johnstonii* from the Coal Mine Quarry by Retallack (1977, Microfiche Frame G12) is doubtful as it was based on fragmentary material. The microsporophylls placed in *Pteruchus johnstonii* from the middle Triassic Benolong assemblage by Holmes (1982) differ from the Nymboida specimens by their shorter, more rounded unpaired heads. *P. feistmantelii* (Holmes 1987 p.172) from the Lorne Basin (Holmes and Ash 1979) and the Sydney Basin (Walkom 1925a, Pl. 31, fig. 10; Retallack 1980) was very much longer and more gracile.

It is interesting to note that in both the Molteno and Nymboida localities where *P. matatimajor* or a comparable form occurs, the leaves of the *D. dubium* complex are the most common *Dicroidium*.

#### *Pteruchus* sp.

Figure 23F

##### Description

A detached microsporophyll, 40 mm long and 9 mm wide; forking distally.

##### Discussion

This microsporophyll is larger than all other Nymboida *Pteruchus* heads and the forking structure is unique. In size it approaches the long gracile microsporophyll of *P. feistmantelii* from the Lorne Basin, Australia (Holmes and Ash 1979).

#### CONCLUSION

Leaves of the *Dicroidium* morpho-genus are the most commonly occurring fossils in the large collections made from the Nymboida quarries. Collections have been made from differing sedimentary facies and may represent vegetation from various habitats depending on the degree of transport or dispersal before burial. The Nymboida leaves ascribed to *Dicroidium* display a wide range of variation and intergrading forms ranging from simple to pinnate to bipinnate. To identify individual leaves with previously described species ignores the presence of the intergrading forms. Therefore we have separated

the leaves into five 'species complexes' each centred on a widely distributed and well-recognised morpho-species. The single leaf of *D. elongatum* present in the Nymboida flora is possibly a transported specimen from a source far beyond the Nymboida flood-plain vegetation which comprises the bulk of the preserved material. Future descriptions of all fossil floras should recognise the variability and range of intergrading forms due to ecological factors, the chance factors involved in the fossilisation process and discovery of the fossilised material.

## ACKNOWLEDGEMENTS

W.B. Keith Holmes acknowledges with appreciation the enthusiastic help by his late wife Felicity and his daughters in collecting specimens from the Nymboida quarries over a period of almost 40 years. The operator of the quarries during that period, the late Mr Brian Foley, always provided valuable assistance during our visits by exposing a never-ending supply of material for examination.

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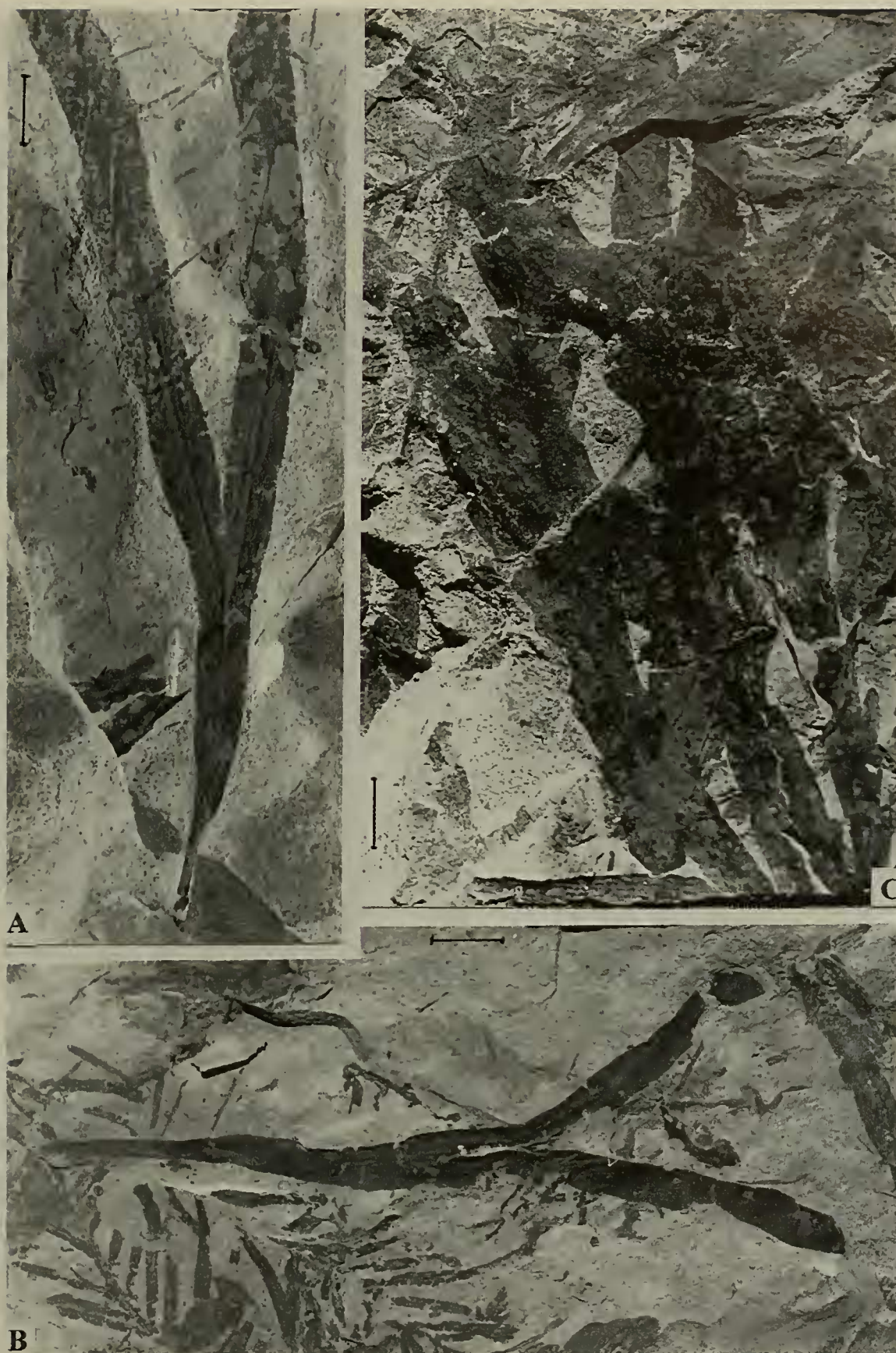


Figure 1. A–C. *Dicroidium coriaceum* complex. Larger leaves with mainly entire margins. A. AMF125016; B. AMF125017; C. AMF125018. Scale bar = 1 cm.



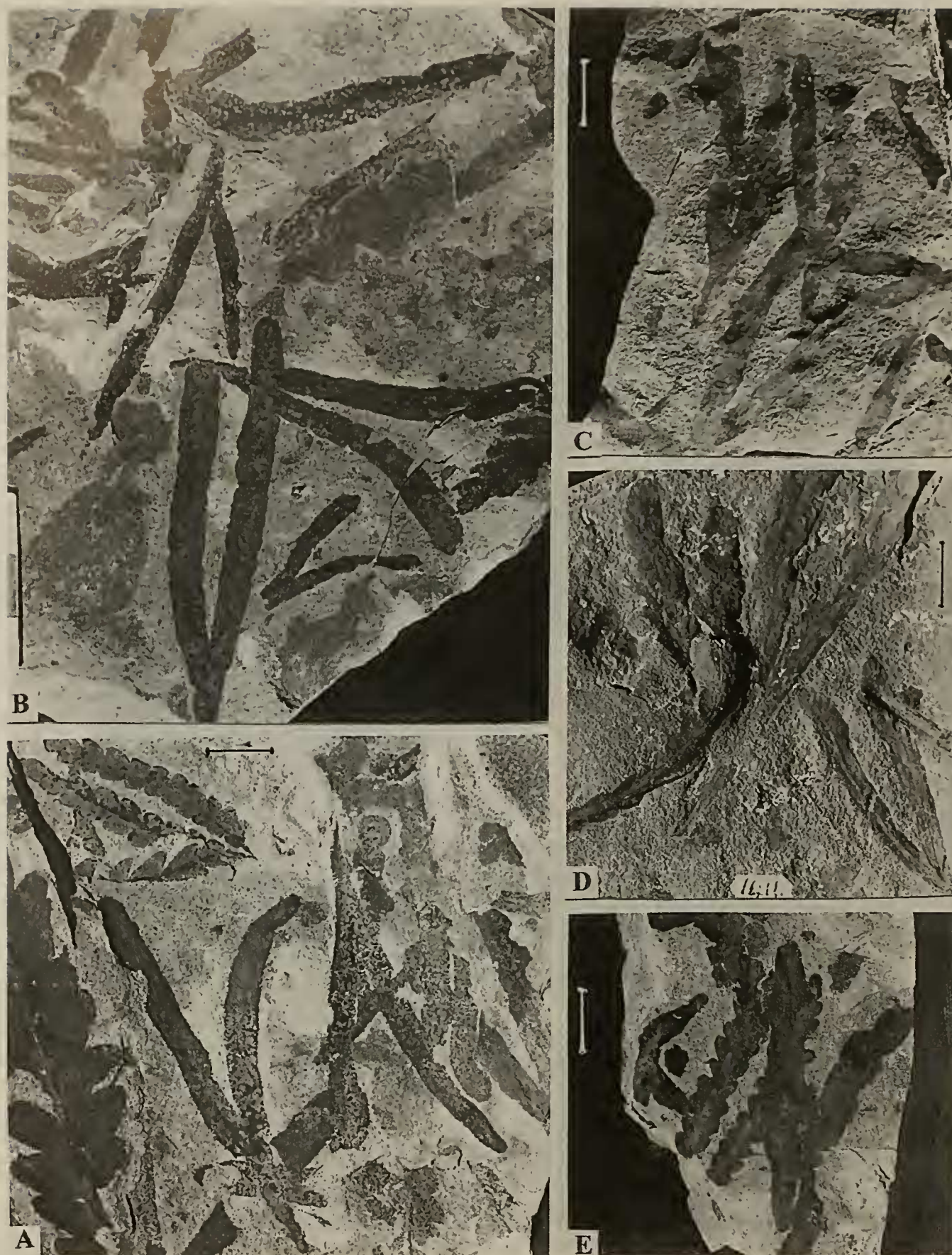


Figure 2. A–E. *Dicroidium coriaceum* complex (excluding the leaf on lower left of Fig. 2A). Smaller leaves with margins ranging from entire to pinnatifid. All specimens from the same slab of siltstone and represent a single population. A. AMF125019; B. AMF125020; C. AMF125021; D. AMF125022; E. AMF125023, pinnatifid leaf on left hand side intergrading with shorter pinnuled forms of the *D. odontopteroides* complex. Scale bar = 1 cm.



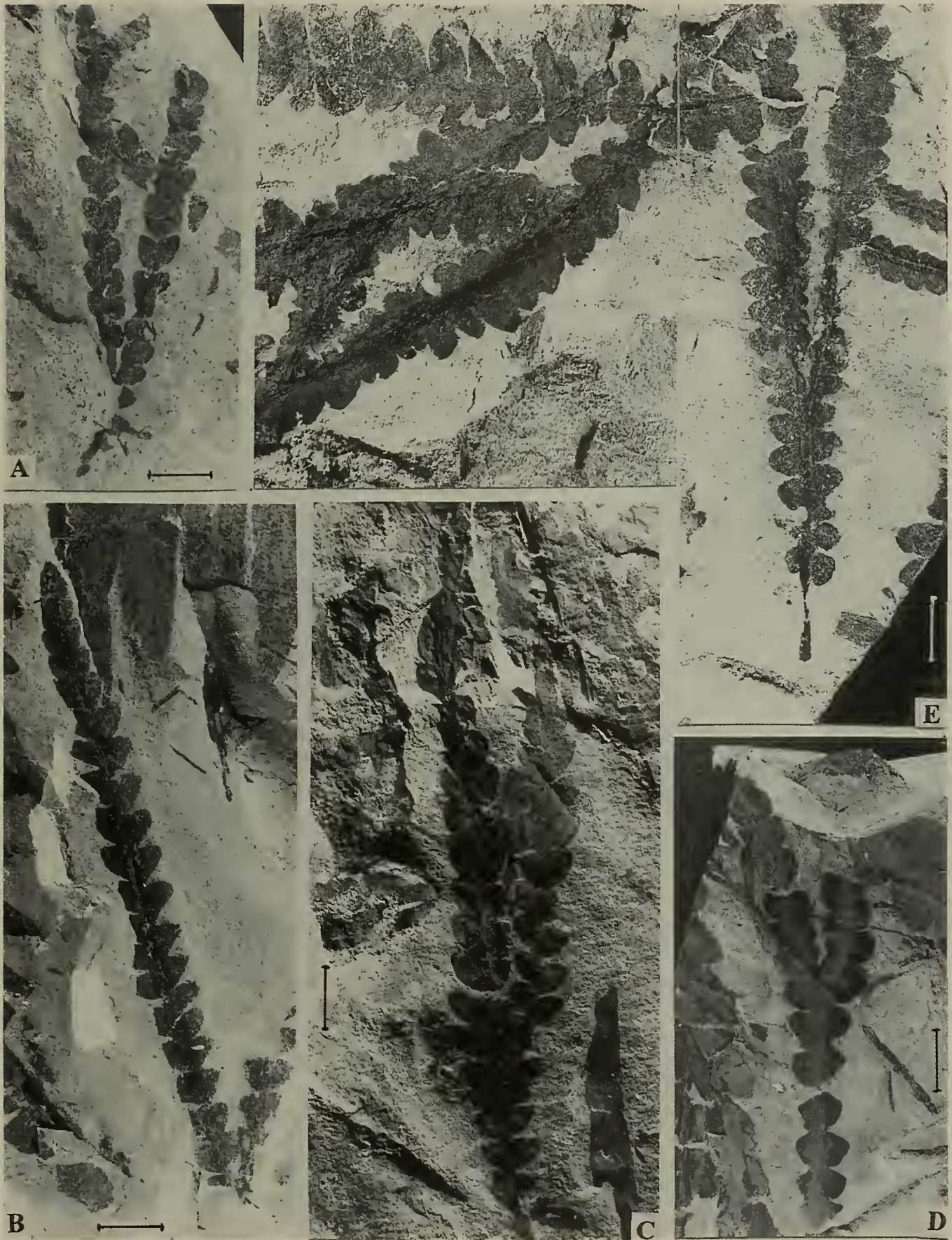


Figure 3. A-E. *Dicroidium odontopteroides* complex. Pinnate leaves with short pinnules. A. AMF125024; B. AMF125025; C. AMF125026; D. AMF125027; E. AMF125028. Scale bar = 1 cm.





Figure 4 A-G. *Dicroidium odontopteroides* complex. Pinnate leaves with short, variously rounded and inclined pinnae. A. AMF125029; B. AMF125030; C. AMF125031; D. AMF125032; E. AMF125033; F. AMF125034; G. AMF125035. Scale bar = 1 cm.





Figure 5 A-D. *Dicroidium odontopteroides* complex. Pinnate leaves forking into 3, 4 or 5 branches. A. AMF125036; B. AMF125037; C. AMF125038; D. AMF125039. Scale bar = 1 cm.





Figure 6. A. *Dicroidium odontopteroides* complex – an assemblage of double-forked leaves demonstrating size and shape variation. AMF125040. B. *Dicroidium dubium* complex – a double forked leaf. AMF125041. Scale bar = 1 cm.



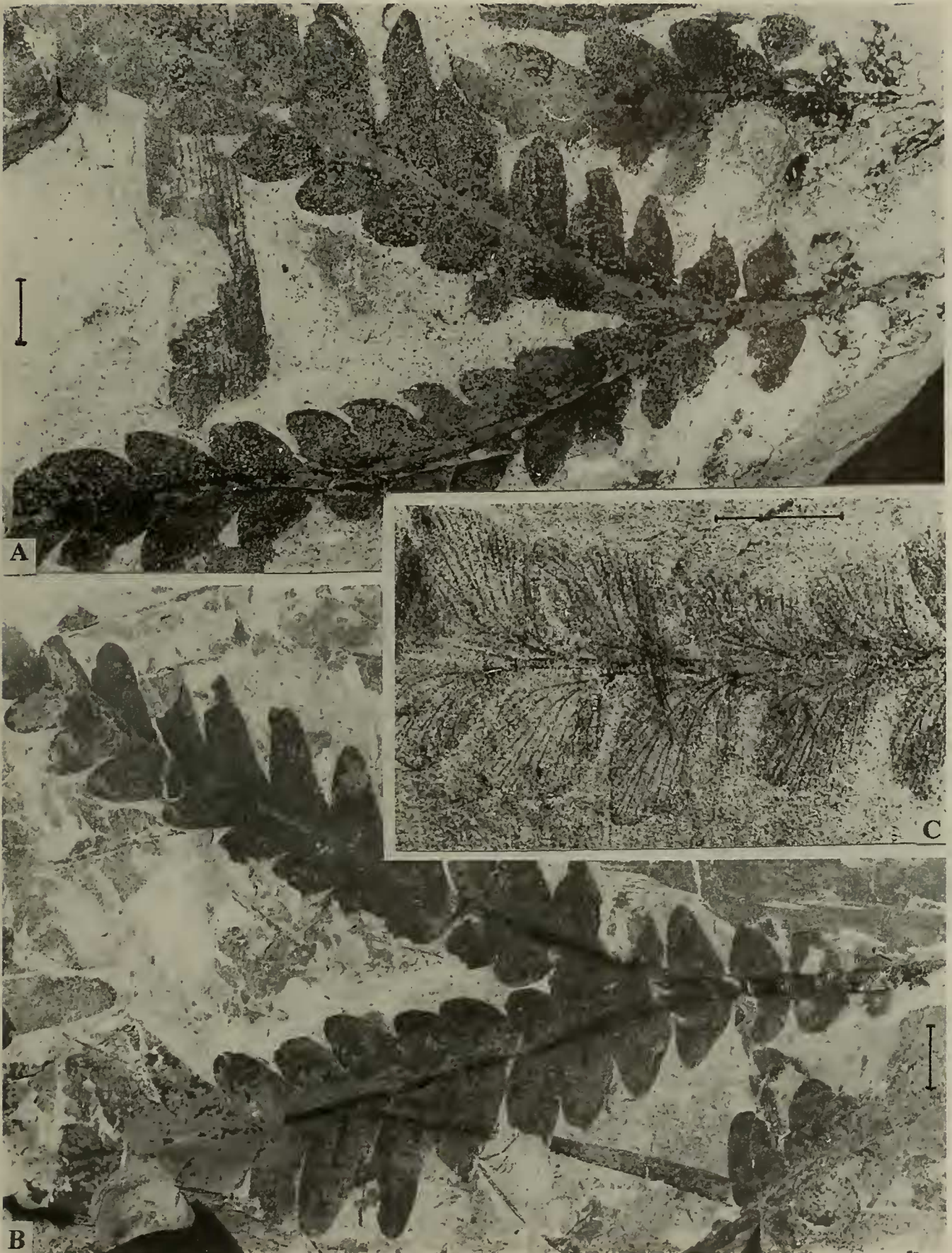


Figure 7. A-C. *Dicroidium odontopteroides* complex. Larger leaves with variously elongated pinnae. A. AMF125042; B. AMF125043. C. AMF125044, leaf showing 'odontopteroid' venation. Scale bar = 1 cm.





Figure 8. A. *Dicroidium odontopteroides* complex. The largest leaf in the complex. AMF125045. Scale bar = 1 cm.





Figure 9. A-C. *Dicroidium odontopteroides* complex. A, B. Forms approaching *Dicroidium lineatum* complex. A. AMF125046; B. AMF125047; C. AMF125048. Scale bar = 1 cm.





Figure 10. A,D,E. *Dicroidium odontopteroides* complex, approaching *Dicroidium lineatum* complex. A. Note portion of *Umkomasia sessilis* strobilus on lower right. AMF125049; D. AMF125050; E. AMF125051. B,C. *Dicroidium lineatum* complex. B. AMF125052; C. AMF125053. Scale bar = 1 cm.





Figure 11. A,B,D. *Dicroidium lineatum* complex. A. AMF125054; B. AMF125055; D. AMF125056. C. Intergrating form between *Dicroidium lineatum* complex and *Dicroidium dubium* complex. AMF125057. Scale bar = 1 cm.





Figure 12. A,D. Forms intergrading between *Dicroidium lineatum* complex and *Dicroidium dubium* complex. A. AMF125058; D. AMF125059. B,C. *Dicroidium lineatum* complex. B. AMF125060; C. AMF125061. Scale bar = 1 cm.





Figure 13. A-C. *Dicroidium dubium* complex showing range of pinna forms. A. AMF125062; B. AMF125063; C. AMF125064. Scale bar = 1 cm.



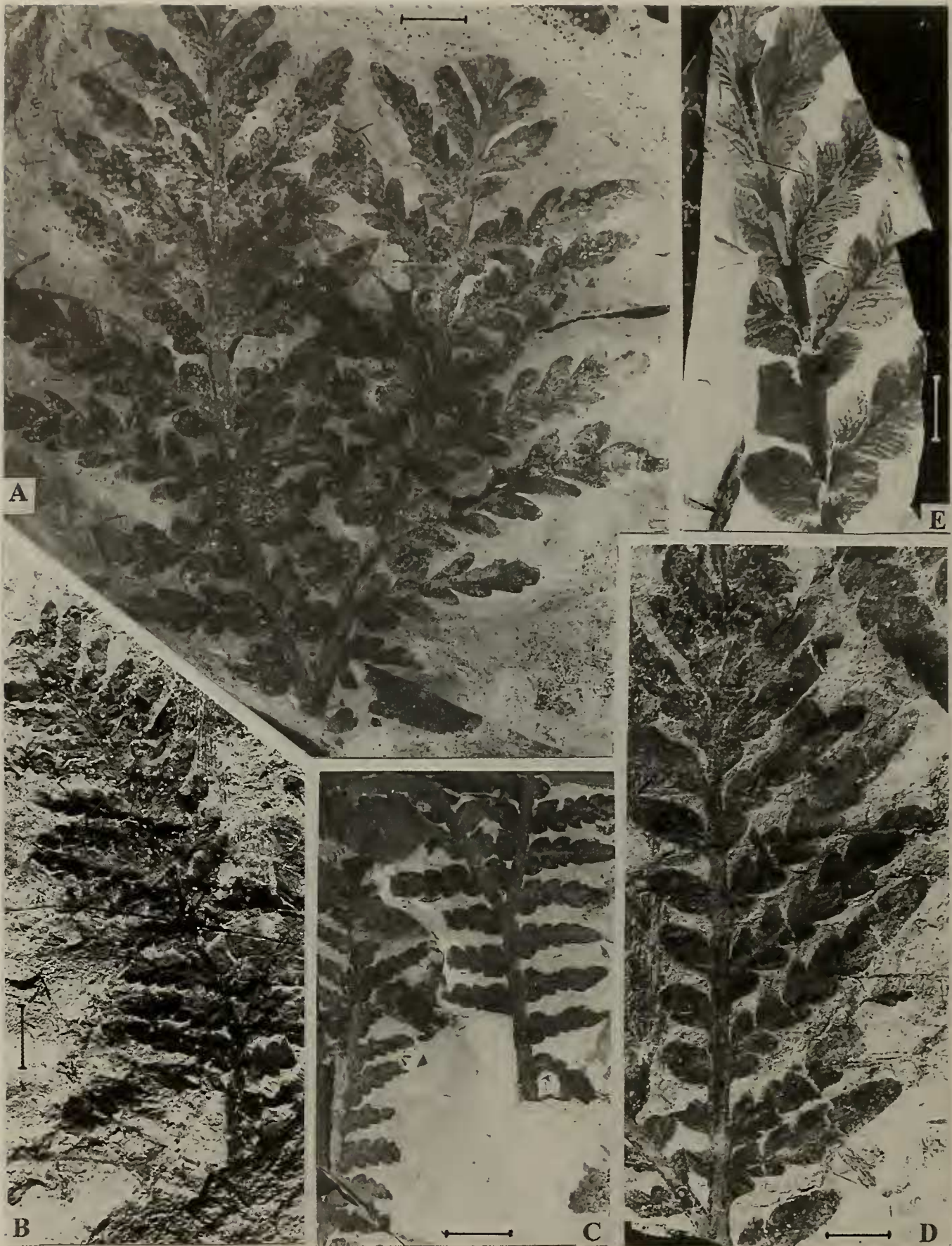


Figure 14. A-E. *Dicroidium dubium* complex. A. AMF125065; B. AMF125066; C. AMF125067; D. AMF125068; E. AMF125069. Scale bar = 1 cm.





Figure 15. A-D. *Dicroidium dubium* complex. A and D approaching *Dicroidium zuberi* complex. A. AMF125070; B. AMF125071; C. AMF125072; D. AMF125073. Scale bar = 1 cm.





Figure 16. A. *Dicroidium dubium* complex- large bipinnatifid form, AMF125074.  
B, C. *Dicroidium zuberi* complex. B. AMF125075; C. AMF125076. Scale bar = 1 cm.



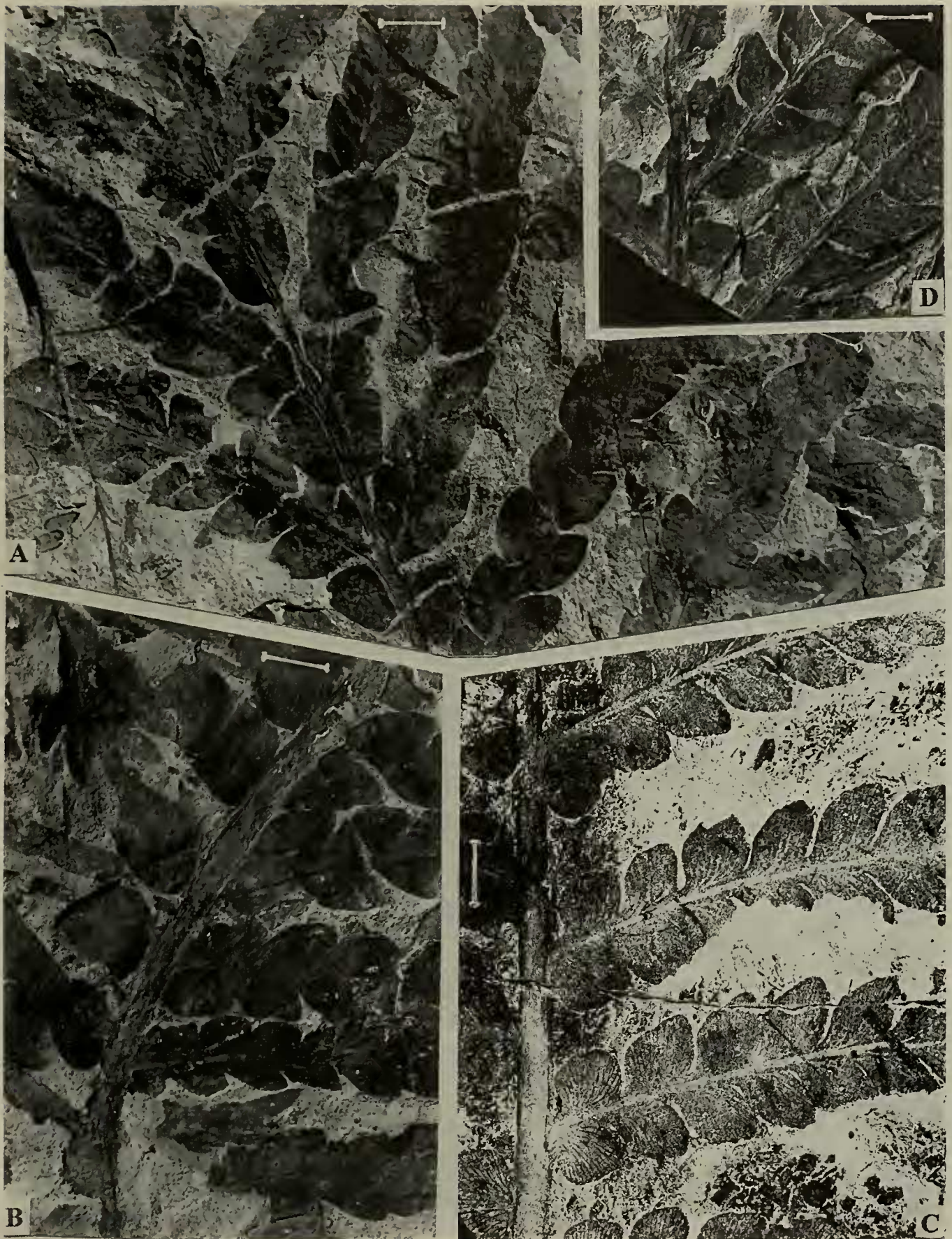


Figure 17. A-D. *Dicroidium zuberi* complex. A. AMF125077; B. AMF125078; C. AMF125079; D. AMF125080. Scale bar = 1 cm.



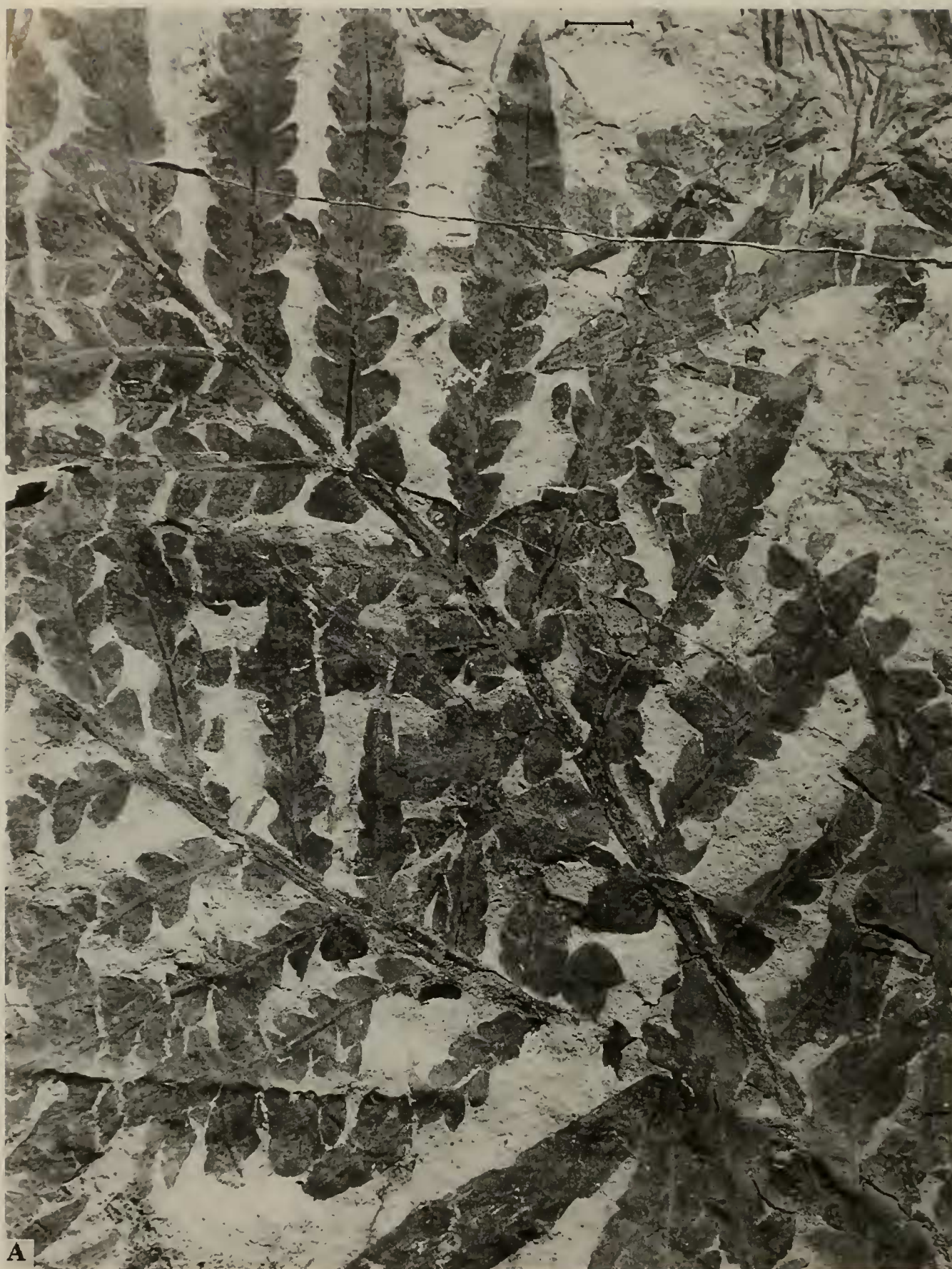


Figure 18. A. *Dicroidium zuberi* complex. AMF125081. Scale bar = 1 cm.





Figure 19. *Dicroidium elongatum* AMF 125082. Scale bar = 1 cm.





Figure 20. A. *Dicroidium elongatum* AMF125082. B. ?*Dicroidium nymboidense* sp. nov. AMF125083. C, D. *Dicroidium* sp. A. C. AMF125084; D. AMF125085. E. *Dicroidium* sp. B. AMF125086. Scale bar = 1 cm.



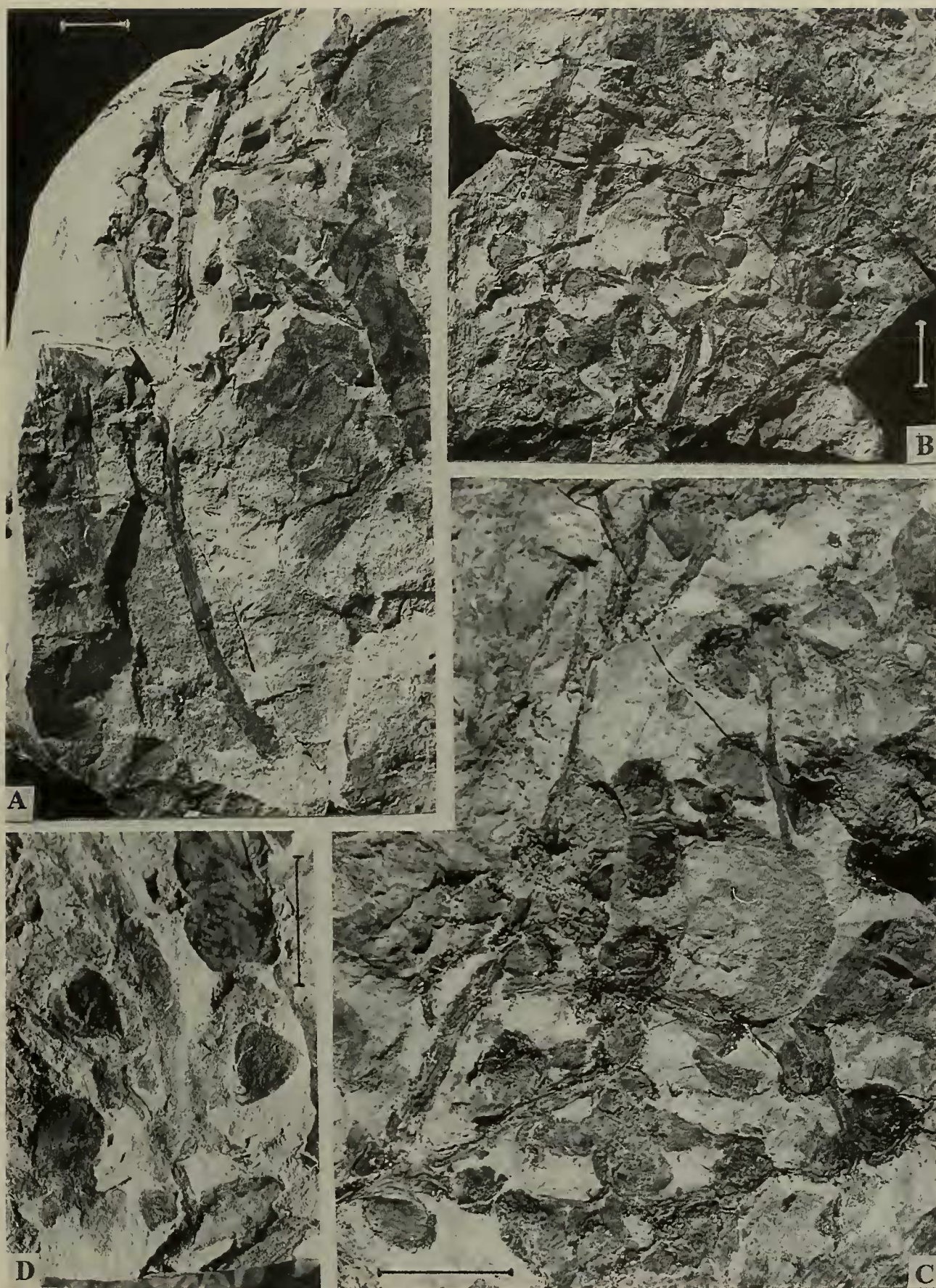


Figure 21. A. *Umkomasia distans*. Holotype. AMF63824. B, C. *Umkomasia sessilis*. B. Holotype AMF63831. C. AMF125087. D. Dispersed *Umkomasia* ovules showing bifid micropyle. AMF125088. Scale bar = 1 cm.





Figure 22. A-C. *Umkomasia* sp. strobili and cupules: A. *Umkomasia distans*. AMF125089. B. *Umkomasia sessilis*. AMF125090. C. *Umkomasia* sp. AMF125091. D-F. *Umkomasia* cupules: D. AMF125092; E. AMF125093; F. AMF125094. Scale bar = 1 cm.



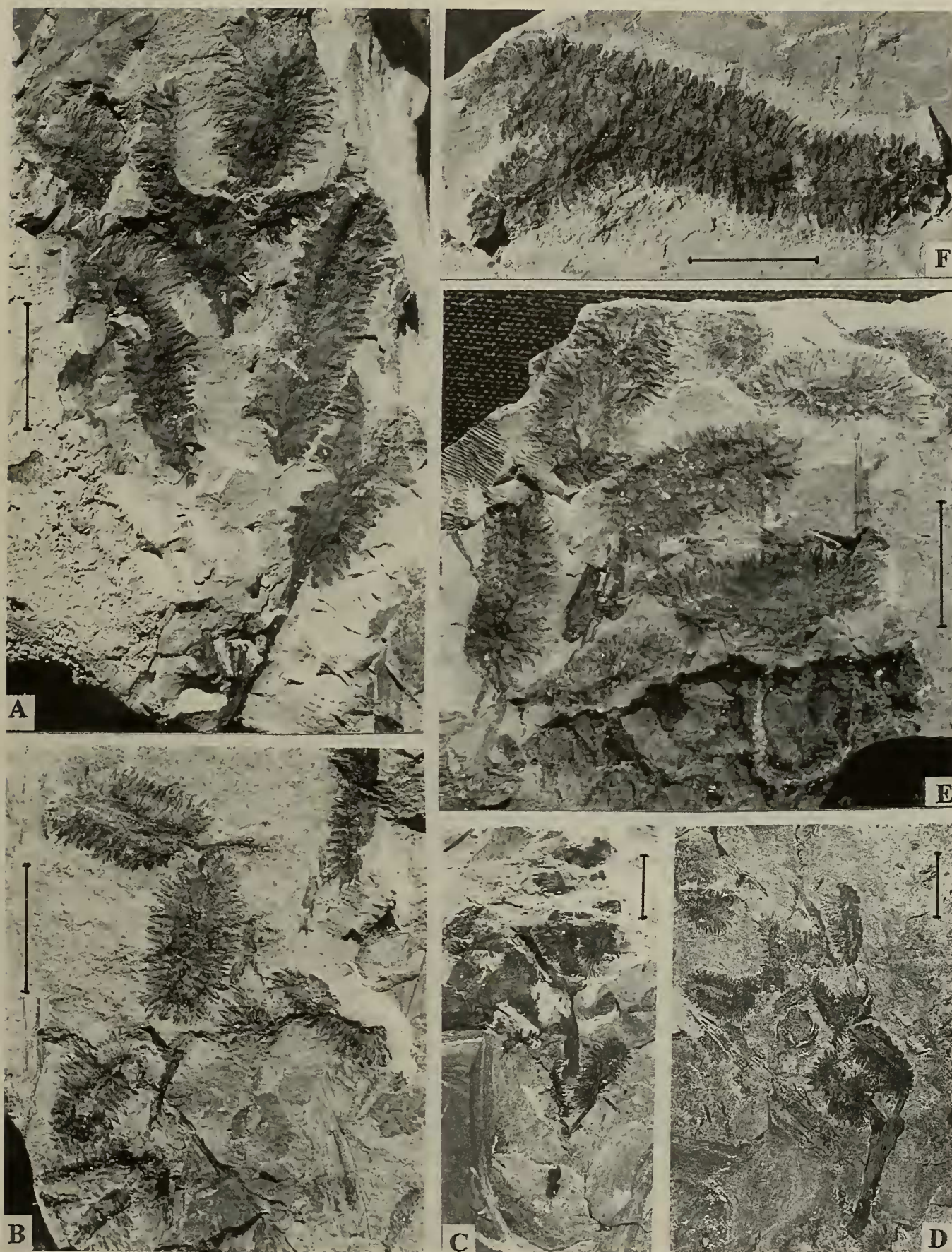


Figure 23. A-E. *Pteruchus* sp.cf. *P. matatimajor* microsporophylls. A. AMF125095; B. AMF125096; C. AMF125097; D. AMF125098; E. AMF125099; F. *Pteruchus* sp. A. AMF125100. Scale bar = 1 cm.